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Dinoflagellate fossils: Geological and biological applications

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ABSTRACT

Dinoflagellates are part of the marine plankton and about 200 species produce a cyst (dinocyst) during their life cycle, these organic-walled sexually-produced cysts being fossilizable in sediments for hundreds of millions of years. Over the past 40–50 years, dinocysts have led to major advances on Mesozoic-Cenozoic research, in terms of biostratigraphy and paleogeogeography. Dinocyst taxonomy has then been continuously revised, with the tabulation being the main morphological link between living dinoflagellates and fossilized cysts. Over the Quaternary, and based on the principle of uniformitarianism (i.e. species ecology did not change through time), relationships between modern assemblages and present-day environmental factors controlling their distribution also allow for dinocyst-based quantitative reconstructions derived from transfer function calculations. This paper presents a non-exhaustive review of the dinocyst literature allowing the reader to get a perspective about how they were discovered and defined, but also how they are applied in (paleo)ecological studies according to the timescale considered allowing then to provide useful insights into the future climate change and its associated ecological repercussions.

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1. Introduction

Dinoflagellates are unusual eukaryotes in many ways and, according to morphology, fossil records, biomarkers and molecular phylogenies, their evolution and origin remain debated up to now. Dinoflagellates have been claimed to be plants (algae) by botanists and animals (protozoa) by zoologists and were classified as such during the XIXth and early XXth centuries. They are biflagellate marine and freshwater protists with vesiculated membranes belonging to the Alveolates and represent the only protist group to have both phototrophic and heterotrophic taxa. Alveolates are supposed to have diverged in the Neoproterozoic; dinoflagellates have been suggested to appear in the Paleozoic based on biomarker or biomolecular evidence, whereas fossil dinoflagellate cysts or dinocysts appear only in the Mesozoic.

Dinoflagellate cysts (cyst-motile stage relationships discussed in Chapter 1) can fossilize in sediments for hundreds of millions of years and have long been used across the Mesozoic-Cenozoic timescale for biostratigraphical and paleogeographical studies (as illustrated in Chapter 2) as well as paleoceanographical studies (see Chapters 3 and 4) including quantitative reconstructions (see Chapter 3). To illustrate the potential of dinocysts in paleoceanographical studies, we focus on the last glacial period in the North Atlantic Ocean that constitutes one of the typical examples of enigmatic features of rapid climate variability (see Chapter 4). Finally, the most recent evolution in Quaternary paleoecology is combining high resolution palynology (see Chapter 5) with ancient DNA on historical time-scales (see Chapter 6). The example is chosen from the Bay of Brest (northwestern France) with the

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estuarine environment of Daoulas that today records more and more intense toxic dinoflagellate blooms linked with the nutrient enrichment (eutrophication) of the aquatic system.

2. Importance of cyst-motile stage relationships for dinoflagellate taxonomy

The existence of two life stages, respectively called the motile stage and the cyst stage, has caused the creation of separate biological and paleontological classification systems. The most recent version of the International Code of Nomenclature for algae, fungi and plants (ICN) stipulates that separate names are allowed for the fossil and living dinoflagellates (or cyst and motile stages, respectively; McNeill et al., 2012). Based on the configuration of the vesicles of the motile stage, the so-called tabulation, dinoflagellates were classified into 14 major orders: Gymnodiniales, Ptychodiscales, Suessiales, Gonyaulacales, Peridiniales, Nannoceratopsiales, Dinophysiales, Prorocentrales, Desmocapsales, Phytodiniales, Thoracosphaerales, Blastodiniales, Noctilucales and Syndiniales (Fensome et al., 1993). Several orders are not discussed here: Nannoceratopsiales are extinct and no cysts are known for some Blastodiniales, Desmocapsales, Noctilucales and Syndiniales.

Resting cysts are known to be produced during the sexual phase; Stosch (1964, 1965, 1972, 1973) indeed demonstrated that sexual processes lead to resting cyst formation in different marine and freshwater species. These sexually-produced cysts, usually organic-walled (dinosporin), can be distinguished from asexual cellulosic resting stages (ecdysal or pellicle cysts; e.g., Bravo and Figueroa, 2014), although a quite diversified set of composition exists for the cyst. Organic-walled cysts consist of a macromolecule, whose chemical composition in phototrophic dinoflagellates suggests a cellulose-like glucan, while heterotrophic forms produce a nitrogen-rich glycan (Bogus et al., 2014). These organic-walled cysts are fossilizable, thus commonly observed in the sedimentary archive, and are found within the Peridiniales, Gonyaulacales, Prorocentrales, Gymnodiniales, Thoracosphaerales (only *Pentapharsodinium* and *Ensiculifera*), Phytodiniales and perhaps Dinophysiales (see below). Calcareous cysts that have an inner organic lining are restricted to the Thoracosphaerales (Gottschling et al., 2012). Modern siliceous cysts are known only for *Ceratium hirundinella* (Chapman et al., 1982).

About 13–16% of dinoflagellates are known to produce resting cysts (Head, 1996). Since then, around 100 new cyst-motile stage relationships have been proposed. As there are now at least 2,294 species of dinoflagellates described (Gómez, 2012), adding these 100 new cyst-motile stage relationships to the 260 listed by Head (1996), suggests that this percentage remains similar, and cyst-motile relationships have kept more or less in line with new species descriptions. However, the exact number still needs to be calculated since not only the new relationships are important, but previously documented cyst-motile stage relationships have been revised (e.g., Lewis et al., 2001) and synonymies between motile stages and cysts have changed (e.g., Gómez, 2012; Williams et al., 2017a). A detailed update of Head (1996) is imminent (Head, pers. comm.).

Also, at least 71 modern cysts have been shown to preserve in the fossil record (Zonneveld et al., 2013; Mudie et al., 2017), which is about a third of known cysts. In some orders of dinoflagellates, cysts are known for many genera, and it is likely that many more will be described in years to come. Within the Thoracosphaerales, many cysts have been described for many genera, particularly for *Scrippsiella*, *Pentapharsodinium* and *Ensiculifera* (e.g., Lewis, 1991, Kobayashi and Matsuoka, 1995), but also for Pfiesteriaceae such as *Pfiesteria* (e.g., Litaker et al., 2002) and the enigmatic benthic genus *Bysmatrum* (Limoges et al., 2015). The discovery of living cysts belonging to the Suessiales was exciting (Montresor et al., 1999). Previously, only long extinct species belonged to that order, and other suessioid cysts have since been described, particularly for the freshwater dinoflagellates (e.g., Calado and Moestrup, 2005; Hansen et al., 2007).

In other orders of dinoflagellates, resting cysts seem to be restricted to certain genera or subgenera. Within the Peridiniales, this is most notable for the genus *Protoperidinium* where many cysts are documented for species with a first apical paraplate that is ortho, while few cysts have been recorded for species with a first apical paraplate that is meta (e.g., a cyst is depicted by Nordli (1951) for *Protoperidinium granii*) or para (e.g., a cyst is recorded by Wall and Dale (1968) for *Protoperidinium latissimum*). Also within the Peridiniales, however, nearly all genera belonging to the diplopsalioideans seem to have cysts (e.g., Liu et al., 2015a). Within the Gonyaulacales, for some genera, resting cysts are undisputable, such as *Gonyaulax*, *Lingulodinium* and *Protoceratium*, whilst for others, no resting cysts have yet been recorded, such as for many planktonic (e.g., *Ceratocorys*, *Goniodoma*) and particularly benthic (e.g., *Coolia*, *Gambierdiscus*) species. Observations of resting cysts belonging to the gonyaulacoid genus *Tripos* (as *Neoceratium*; Gómez et al., 2010) are remarkable, and seem to suggest that these cysts have been overlooked, and might be fragile or short-lived, and hence not easy to discover. For the Gymnodiniales, resting cysts have been described for many genera such as *Polykrikos*, *Gyrodinium*, *Gymnodinium*, *Barrufeta* and *Akashiwo* (e.g., Matsuoka, 1988; Sampedro et al., 2011; Gu et al., 2015) but are not known for other resting cysts (e.g., *Karenia*, *Takayama*, *Nematodinium*). For the Phytodiniales, resting cysts have been recorded for several genera (e.g., *Hemidinium*, *Spiniferodinium*) but not for others (e.g., *Hypnodinium*, *Manchudinium*). It is remarkable that for some orders of dinoflagellates, no resting cysts have been recorded with certainty. This is particularly true for Dinophysiales where cysts have been observed but have to be treated with caution. These have never been observed to be formed in culture and have never been hatched (review by Reguera et al., 2012). Within the Prorocentrales, cyst observations within *Prorocentrum* remained long doubtful, but a recent study has unambiguously showed that cysts exist for the benthic species *Prorocentrum leve* (Mertens et al., 2017a). A major problem with cyst-motile stage relationships is that incubation and culturing experiments can never provide evidence that a particular motile stage of a species does not produce a cyst. Therefore, it is possible that, for some species, cyst production could have been switched off, or their biogeochemical pathways could have changed, during dinoflagellate evolution. For example, Ceratiaceae are recorded from Early to Late Cretaceous, and their gap in the fossil record at the end of Cretaceous may be explained by a transition from resistant dinosporin-based cysts to unpreservable siliceous/cellulosic resting cysts, present in extant Ceratiaceae (Wall and Evitt, 1975; Chapman et al., 1982; Gómez et al., 2010). It is hoped that genetic studies like gene expression ones might reveal such mechanisms. Another problem is that for many modern cyst species found in surface sediments, no motile stage is yet known (e.g., *Melitasphaeridinium choanophorum*; Price et al., 2017a). This is particularly true for oceanic species (*Nematosphaeropsis*, *Impagidinium*) which are rarely seen with cell contents and are difficult to hatch. Some species seem to be endemic and restricted in distribution and therefore the establishment of the cyst-theca relationship occurred only recently (*Dapsilidinium pastielsii*; Mertens et al., 2014).

Cyst morphology is generally species-specific. Within the Peridiniales, species are easily distinguished using cyst morphology (e.g., Wall and Dale, 1968; Harland, 1983), which has been thoroughly studied specifically for the spiny round brown cysts (Radi et al., 2013). For gonyaulacoids, cyst morphologies allow

species identification particularly for *Gonyaulax* (e.g., Rochon et al., 2009). One gonyaulacoid exception is *Alexandrium catenella* and *Alexandrium tamarense* that have been related to the same cyst morphology (Fukuyo, 1985), while for other *Alexandrium* species, the cyst morphology is useful to separate different species (e.g., Bolch et al., 1991). Within Thoracosphaerales, cysts are also informative up to the species level (e.g., Lewis, 1991). An exception however exists with *Scrippsiella trochoidea* which was shown to exist out of several cryptic species with very similar morphologies of motile and cyst stages (Montresor et al., 2003), questioning what is the true *Scrippsiella trochoidea* (Zinssmeister et al., 2011). For some orders, cyst morphology is also helpful in generic classification. This is particularly true for the Peridiniales, where superficially similar species belonging to the genus *Protoperidinium* have such different cyst morphologies that they are classified within different cyst-based genera (e.g., *Quinquecuspis*, *Trinovantedinium*, *Votadinium*, *Brigantedinium*; Harland, 1983). First attempts to understand the combined evolution within Peridiniales suggest that molecular phylogenies reflect well the sections within *Protoperidinium*, as well as the related cyst-based genera (e.g., Matsuoka and Kawami, 2013; Gu et al., 2015; Mertens et al., 2017b). For the diplopsaloideans, cyst morphology is also genus-specific (e.g., Liu et al., 2015b), although nearly no cyst-based names have been erected (e.g., Matsuoka, 1988), presumably because these cysts are difficult to identify up to the genus or species level in the fossil record. Within Gonyaulacales, the motile-based genus *Gonyaulax* can be subdivided into different cyst-based genera (e.g., *Spiniferites*, *Bitectatodinium*, and *Impagidinium*), although molecular phylogenies are still in an early stage and need more sequences (Mertens et al., 2017c). Two issues with dual nomenclature in gonyaulacoids were recently identified. First, Mertens et al. (2017c) have shown that the motile species *Gonyaulax baltica* can be related to two cyst genera: *Impagidinium* and *Spiniferites* (heterospory). Second, Mertens et al. (2018) showed that the cyst *Operculodinium* can be related to two motile genera *Protoceratium* and *Pentaplacodinium*. These discrepancies between motile-based and cyst-based taxonomies are not easily resolved and have led to debates regarding dual nomenclature (Ellegaard et al., in press). Future morpho-molecular works will perhaps help resolve such issues. At higher taxonomic levels, it often becomes more difficult to evaluate the value of cysts. Indeed, in molecular phylogenies, affinities between genera and species are revealed with significant bootstrap support, and more basal nodes in phylogenies have often no significant bootstrap values (e.g., Daugbjerg et al., 2000; Saldarriaga et al., 2004). Concatenated phylogenies (e.g., Orr et al., 2012; Gottschling et al., 2012) and transcriptomics (e.g., Janouškovec et al., 2016; Price and Bhattacharya, 2017) can increase the support of these basal nodes, and are promising techniques to evaluate the classification proposed by Fensome et al. (1993). For instance, transcriptome-based phylogenetic trees of Janouškovec et al. (2016) suggest that a late acquisition of dinosterol in the dinoflagellate group is inconsistent with dinoflagellates as being the source of this biomarker in pre-Mesozoic strata. They proposed a revised model for the evolution of thecal tabulations, the monophyly of thecate dinoflagellates (Peridiniales, Gonyaulacales, Prorocentrales) and the paraphyly of athecate ones (Gymnodiniales).

3. Dinocysts as powerful biostratigraphical proxies

3.1. Acritarchs and dinocysts

Ehrenberg (1836) was the first author to recognize fossil dinoflagellate cysts in thin flakes of Cretaceous flints. He observed tabulation and flagellar furrows and compared those to the living planktonic genus *Peridinium* and erected a new species *Peridinium pyrophorum* (now *Palaeoperidinium pyrophorum*). He also observed spiny bodies bearing variable spine morphologies, and considered these to be Desmids (e.g. extant freshwater green algae, Zygnematophyceae) and described *Xanthidium ramosum* (now *Spiniferites ramosus*). The term "Xanthidia" named all these spiny bodies during almost a century. Deane (1845) and Reinsch (1905) suggested that "Xanthidia" were not Desmids and Wetzel (1933) erected the genus *Hystrichosphaera* with both *H. furcata* and *H. ramosa* as type species. Nevertheless, their affinity remained unknown and Deflandre (1936) regarded Hystrichospheres as *Incertae sedis*. As "Xanthidia", the term "Hystrichosphere" became popular and was used for spiny bodies until 1960. The first clear interpretation of the relation between dinoflagellate thecae and cysts and the demonstration that hystrichospheres are dinoflagellate cysts were suggested through meticulous morphological comparison on 119 genera (Evitt, 1961). He observed that the openings of dinoflagellate cysts are regular in form and position and correspond to a plate or group of plates. He created the name archeopyle (Evitt, 1961) to define the angular germinal opening of cysts. By the precise study of variable hystrichosphere processes, he showed that their number and size are related to the number and size of thecae plates. These hystrichospheres have indeed to be interpreted as planozygotes formed within thecae.

From 1964 to 2012, *Arpylorus antiquus* (Calandra, 1964) was considered by many as the first non-controversial dinocyst described from the Silurian of southern Tunisia. The common dinoflagellate tabulation was described in the folded vesicle through the quadrangular form of the aperture split into plate-like fragments, and these elements were used to interpret *A. antiquus* as a dinocyst (Evitt and Davidson, 1964; Sarjeant, 1978; Stover and Evitt, 1978; Lentin and Williams, 1981). Nevertheless, many researchers questioned the absence of cingulum and sulcus marks (Bujak and Williams, 1981; Bujak and Davies, 1983; Evitt, 1985). Le Herissé et al. (2012) studied the type material and concluded that *A. antiquus* is not a dinocyst. Indeed, the large development of a fine membrane at the periphery of vesicles, and the composition of the wall (analyzed with a Fourier transform infrared [FTIR] microspectroscopy) made of a biopolymer not consistent with dinosporin or dinosterane, led these authors to conclude that *A. antiquus* would rather represent a storage structure produced by invertebrates such as eurypterids ("sea scorpions").

Much later, during the Triassic, a time of appearance and diversification of many fossil groups, organic-walled microfossils undoubtedly related to dinocysts appeared in the Ladinian, Middle Triassic, around 240 Ma (Fensome et al., 1996). Dinoflagellates evolved rapidly to fill the niches left vacant after the Permian-Triassic mass extinctions and the radiation of dinoflagellates during the Middle Triassic to the Middle Jurassic has been a real evolutionary process (Fensome et al., 1996a). Mesozoic explosion and diversification of the overall species abundances and genera were linked to the increasing global sea level resulting in large number of shallow coastal shelves (MacRae et al., 1996). The earliest dinocyst forms wore numerous latitudinal paraplate series. The fossil record indicates a general trend in the reduction of series, and the main extant counterpart orders, Gonyaulacales and Peridiniales, appeared during the Early Jurassic.

However, although microfossils with all morphological characters of dinocysts only appear in the early Mesozoic, many Paleozoic palynomorphs, mostly assigned to the acritarchs, have strong morphological similarities with dinocysts, but also similar paleogeographical or paleoecological distribution patterns. Indeed, Evitt (1963) created the term acritarchs for all those "hystrichospheres" that could not be attributed to dinocysts, i.e. all organic-walled microfossils displaying splits or simple circular openings, but without groove marks and with morphologies different from those of dinoflagellates and other living organisms (Fig. 1a). The acritarchs

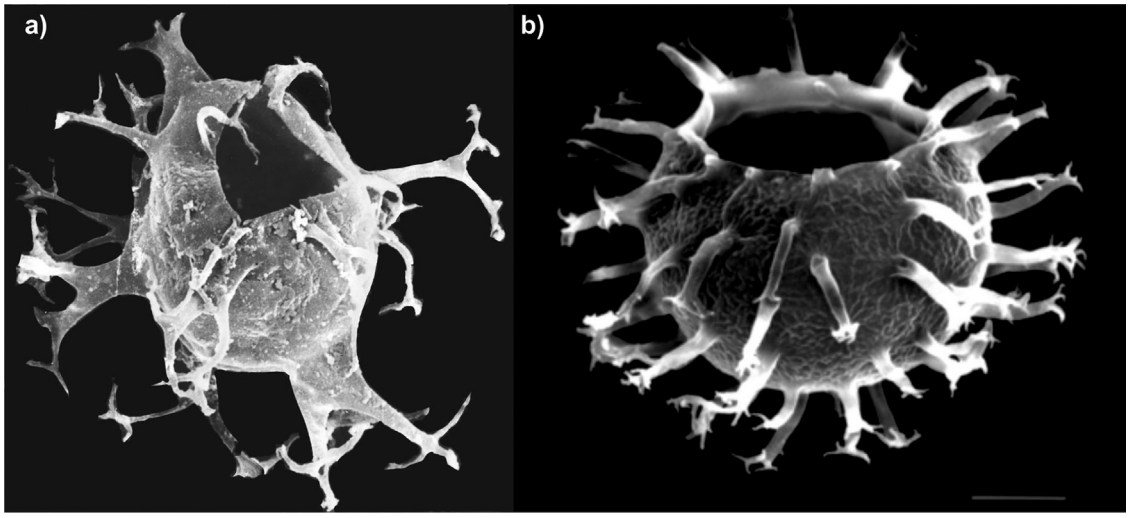

Fig. 1. Dinocyst from the mid-Cretaceous *Achomosphaera ramulifera* (Campanian). Note the archeopyle (precingular) with angular boundaries (plate boundaries). Bifide and trifide processes are located on bifide and triple junctions. Photo: Edwige Masure; b) Galeate acritarch *Stelliferidium sp*. Note the opening without angular marks and the absence of cingulum and sulcus. Photo: Marco Vecoli.

are, by definition, of unknown origin (*Incertae sedis*), known from the Proterozoic and throughout the Phanerozoic. Acritarchs probably include a high variety of biological groups, and not all of them should be considered as cysts of microphytoplankton. In addition, not all acritarchs are marine. Simple acritarchs have been found since the Archaean 3200 Ma (Javaux et al., 2010) and are most probably not related to dinocysts. A study of openings and process distributions in Early Paleozoic acritarchs led Lister (1970) and Bujak and Williams (1981) to suggest that some of these acritarchs could be dinocysts (e.g., *Cymbosphaeridium*). Organisms with probable dinoflagellate affinity have been reported from Neoproterozoic (i.e. 900 to 800 Ma, Butterfield and Rainbird, 1998) and Leppig and Montenari (2000) subsequently suggested the term "protodinoflagellates". Galeate acritarchs (Servais and Eiserhardt, 1995), from the Cambrian-Ordovician transition, are interpreted as resting cysts of microorganisms similar to dinoflagellates (Servais et al., 2004): similar size ranges and process morphologies, the presence of an archeopyle-like opening and of a tabulation-like pattern on the vesicle wall, strongly resemble those of dinocysts (Fig. 1b). In terms of biomarker studies, the presence of dinosteranes 4-methyl-24-ethylcholestane, commonly associated with dinoflagellates cysts, in Precambrian, Cambrian and Paleozoic kerogens led Moldowan et al. (1996), Moldowan and Talyzina (1998) and Talyzina et al. (2000), to propose that some acritarchs were related to dinoflagellates, originating from late Precambrian, and were probably already common in the early Paleozoic.

3.2. Taxonomic tools and dinocyst classification for biostratigraphy

Useful taxonomic tools have been developed, known as the Eisenack Catalogs (Eisenack and Klement, 1964; Eisenack and Kjellström, 1972), and then followed by new series of five volumes (e.g., Fensome et al., 1991). Indexation of fossil dinoflagellates at generic, specific and intraspecific level has been compiled in the Lentin and Williams Indexes by Lentin and Williams (1973, 1993), followed by Fensome and Williams (2004) and Williams et al. (2017b). These authors developed database systems: Dinoflaj1 (based on the Lentin and Williams Index of fossil dinoflagellates 2004 Edition; Fensome and Williams, 2004), Dinoflaj2 (Fensome et al., 2008) and Dinoflaj3 (Williams et al., 2017b). In addition, a compilation of genera based on archeopyle types was developed by Stover and Evitt (1978), and guides with new holotype illustrations and determination keys were published by Jan du Chêne et al. (1986) and Fauconnier et al. (2002). During the 1960s, authors attempted to merge classification of fossil taxa with the biological classification of modern dinoflagellates (Eisenack and Klement, 1964; Norris and Sarjeant, 1965; Vozzhennikova, 1967), taking into account earlier morphological concepts (proximate, chorate, cavate cysts, with archeopyle types). Evitt suggested that the fundamental building blocks of classification of fossil dinoflagellates are the tabulation; his concepts strongly influenced subsequent authors (Wall and Dale, 1968; Norris, 1978; Harland, 1982). A progressive increase in the phylogenetic component has been developed successively by Wall and Dale (1968), Williams (1977), and Dörhöfer and Davies (1980). Eaton (1980) and Taylor (1980) suggested two new systems to explain relationships and evolution within Peridiniales. From a primitive model (Taylor, 1980) and the migration of plates, Evitt (1985) suggested hypothesized derivation of quinqueform and sexiform tabulations within Gonyaulacacea. A unified classification of fossil and modern dinoflagellates has been established by Fensome et al. (1993).

Before World War II, pioneers (Deflandre, 1937, 1938; Eisenack, 1938) produced substantial publications concerning Cretaceous and Jurassic dinocysts. These microfossils have subsequently been used in petroleum exploration, and a significant number of publications were dedicated to the description of new taxa (Deflandre and Cookson, 1955; Cookson and Eisenack, 1958, 1960), and to dinocyst assemblages related to stages and stratotypes (Foucher, 1979, 1985; Sarjeant, 1979; Davey and Verdier, 1973). First dinocyst charts, based on outcrop samples, were published during the 1950s, and biostratigraphy was successfully used for years by combining dinocyst data with data from ammonites (Sarjeant, 1965; Monteil, 1992a, b, 1993), foraminifera (Gruas-Cavagnetto et al., 1988, Powell, 1992a), calpionelles and nannofossils (Van Hinte, 1976a, b; Vail et al., 1977; Hardenbol and Berggren, 1978). Zonations, First and Last Appearance Data (FAD and LAD), were indeed used to produce stratigraphically robust basin-wide correlations for distinct events. A synthesis was first published for the Jurassic by Woollam and Riding (1983), and then for Mesozoic and Cenozoic timescales (Williams and Bujak, 1986; Powell, 1992b; Williams et al., 1993). For the northern hemisphere, two paleoprovinces have been reported, the tethysian and boreal domains; few dinoflagellate biozonations can thus be considered for large areas during the Cretaceous. For the southern hemisphere, a biostratigraphical synthesis was published by Helby et al. (1987) and

Williams et al. (2004). Haq et al. (1987) also provided a Mesozoic and Cenozoic chart with microfossil biozones and dinoflagellate bio-horizons, through third order stratigraphic sequences. Sedimentologists and stratigraphers then built, for the Mesozoic and Cenozoic Sequence Stratigraphy of European Basins Project, a documented chronostratigraphy and outcrop record of depositional sequences calibrated across a large number of stratotypes (de Graciansky et al., 1999; Fensome et al., 2009). The Geologic TimeScale (GTS) Foundation provides information about dinoflagellate and acritarch FAD and LAD, as well as for other microfossils with standard chronostratigraphy (Ogg et al., 2008). Also, regarding more specifically the Cenozoic interval, typical Paleogeone dinocysts indicative of environmental conditions were compiled in Pross and Brinkhuis (2005). Paleocene and Eocene periods often include discussions on the specific Paleocene Eocene Thermal Maximum (PETM) event, representing a phase of global warming with massive CO_2 inputs into the climate system, then implying extreme ecosystem variability (e.g., Frieling et al., 2018). Dinocyst stratigraphy for the Neogene in northern latitudes, and more precisely for the Oligocene-Miocene, is discussed in Schreck et al. (2017) and Bijl et al. (2018), respectively. Also, phase relationships between climate forcing and paleoecological responses across the Pliocene (De Schepper et al., 2015), Plio-Pleistocene climate transition (Hennissen et al., 2016), or Pleistocene glacial-interglacial stages (Donders et al., 2018) have also recently been discussed even if ecological optima of extinct species are not always well known, challenging the use of quantitative sea-surface reconstructions (cf. following chapter 3 of this manuscript). Indeed, although some species ecology has remained similar through the Neogene, especially across the Miocene and Pliocene (e.g., De Schepper et al., 2015; Hennissen et al., 2016; Schreck et al., 2017), dinocyst assemblages do not always find analogues in modern sediments. Across the Paleogene-Neogene timescale, dinocyst-based interpretations then often remain qualitative, but paleohydrological reconstructions on the pre-Quaternary period are tentatively calibrated through crossed geochemical-palynological information allowing for instance to infer temperature ranges for extinct taxa (e.g., Schreck et al., 2017; Frieling and Sluijs, 2018).

4. Modern dinocyst distribution and transfer function approaches

The use of dinocysts as a proxy for Quaternary paleoclimate and paleoceanographic reconstructions is based on the principle of uniformitarianism, i.e. species ecology did not change through the Quaternary timescale. This fundamental concept is based on relationships between dinocyst assemblages and environmental factors controlling their distribution (e.g., Marret and Zonneveld, 2003; Zonneveld et al., 2013), i.e. between modern assemblages from core tops (or first centimeter of interface cores) and modern-day observations (instrumental data of sea-surface conditions). This step is a pre-requisite for quantitative reconstructions derived from transfer function calculations (e.g., Guiot and de Vernal, 2007).

4.1. Worldwide dinocyst distribution in modern sediments

The modern distribution and the taxonomy inventory of modern dinocyst species have been well documented through regional *in situ* studies of sediment traps and/or surface sediment samples since the 1960–70s (e.g., Wall, 1965; Wall et al., 1977; Williams, 1971; Harland, 1983, Turon, 1984; Dodge and Harland, 1991; Marret, 1994; Marret and de Vernal, 1997; Rochon et al., 1999; Zonneveld et al., 2001; Radi and de Vernal, 2004; Pospelova et al., 2005; Holzwarth et al., 2007; Bouimetarhan et al., 2009; Price and Pospelova, 2011; Limoges et al., 2013; Price et al., 2016; Mudie et al., 2017). Several of these studies constituted the basis for the first global Atlas of Recent dinoflagellate cyst distribution (835 modern assemblages), depicting worldwide distribution of 61 species (Marret and Zonneveld, 2003). An updated version then included 71 taxa in 2,405 samples (Zonneveld et al., 2013; Fig. 2). A regional Atlas from the Marmara Sea to the

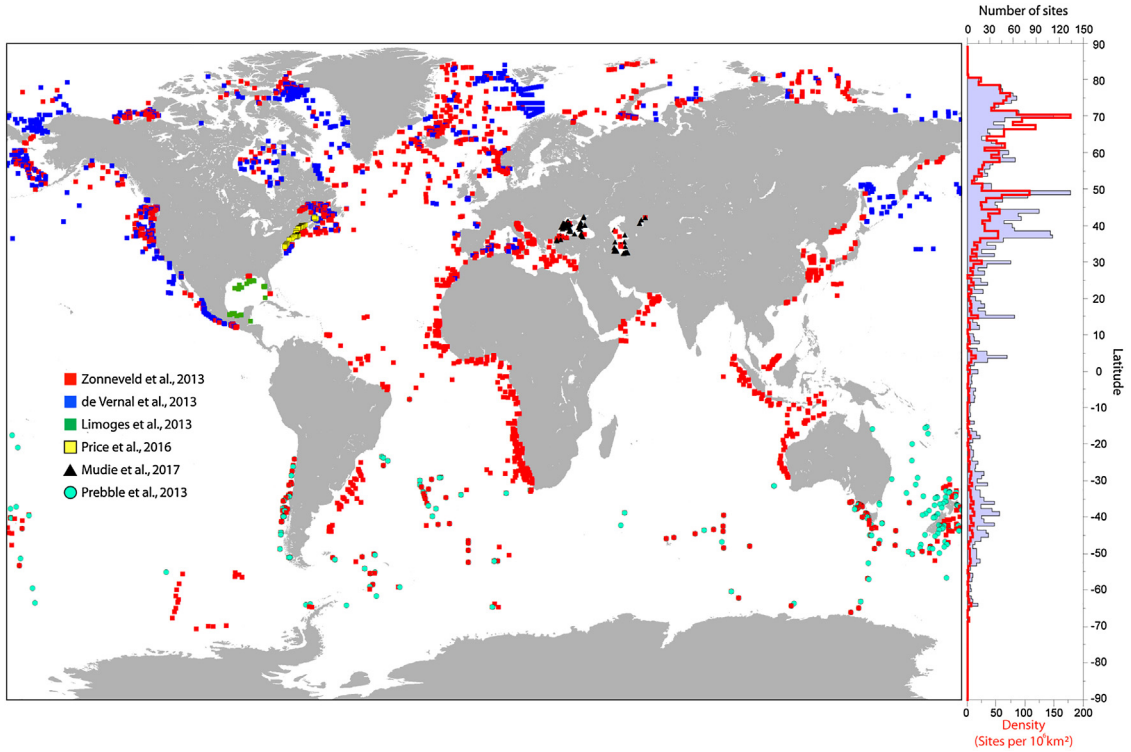

Fig. 2. Location of recently studied modern dinocyst assemblages per atlas, with the spatial distribution and the density of studied sites per latitude.

Caspian Sea (Mudie et al., 2017; Fig. 2) has enabled to further extend our knowledge on the ecological/environmental affinities of most of the dinocyst species routinely used for paleoceanographic investigations. However, gaps remain, in particular in pelagic regions of the Pacific, Indian and Southern oceans (Fig. 2). Despite this incomplete coverage, worldwide modern dinocyst distribution highlights strong relationships between taxa and specific sea-surface conditions, and allows for a better understanding of ecological affinities of several dinocysts. Such atlases also point to the large contrasts between: i) cosmopolitan taxa with large environmental tolerances (i.e. found in most study sites), such as *Brigantedinium* spp. and *Operculodinium centrocarpum* sensu Wall and Dale, 1966 (also *Spiniferites ramosus* or *Impagidinium aculeatum*; Fig. 3) and ii) inversely, species with a narrow distribution (i.e. restricted to specific surface conditions), such as *Islandinium minutum* and *Selenopemphix antarctica* (Fig. 3). Furthermore, the highest taxa diversity observed in the northern hemisphere, especially around 60–65°N with more than 70 taxa per assemblage (Fig. 3), represents a considerable strength for the dinocyst proxy regarding paleoceanographic reconstructions, such as for diatoms, since these regions are often characterized by low foraminiferal diversity or even monospecific assemblages, with carbonates being partly dissolved under low sea-surface temperatures (Kucera, 2007; Eynaud, 2011; Manno and Pavlov, 2014).

4.2. Dinocyst-based Modern Analogue Technique

Paleoceanographic transfer functions were first developed for foraminiferal and radiolarian assemblages, using Q-mode factors, which allow grouping species according to specific water mass conditions (Imbrie and Kipp, 1971), and then linearly linking these groups to sea-surface conditions. However, unimodal response curves between a specific taxon and a specific hydrological parameter cannot be established (Marret and Zonneveld, 2003; Zonneveld et al., 2013), due to the complex ecology and/or large environmental tolerance for some dinocyst taxa and restricted distribution for others. Instead, the Modern Analogue Technique (MAT) was first developed (Hutson, 1980; Prentice, 1980) and applied in palynology to pollen assemblages (Guiot, 1990). Dinocyst assemblages have then also proven to be an advantageous tool to quantitatively assess sea-surface conditions (e.g., de Vernal et al., 1993, 2001, 2005, 2013a, b; Guiot and de Vernal, 2007, 2011; Radi and de Vernal, 2008), even if some critics argued for the large uncertainties in reconstructing summer temperature and sea ice cover also questioning the non-independency of winter temperature and salinity (Telford et al., 2004; Telford and Birks, 2005, 2009, 2011; Telford, 2006). In contrast to the Q-mode factor transfer function, the MAT estimates conditions within the range of the observed oceanographic dataset. This method assumes that modern dinocyst assemblages analyzed in bottom sediments are linked to the overlying oceanographic conditions. Modern oceanographic conditions such as annual and seasonal sea-surface temperature (SST) and salinity (SSS), duration of the sea-ice cover (SIC) and Net Primary Productivity (NPP), are thought to be the predominant primary factors controlling dinoflagellate populations. Observed measurements are then extracted from the World Ocean Atlas, National Snow and Ice Data Center and NASA's Ocean's Color space programs for sea-surface conditions (Table 1). The MAT is based on a similarity matrix, and the statistical distance between the fossil analyzed and all modern analogues existing in the dinocyst database (Table 2) determines the reconstruction of the sea-surface conditions (Guiot and de Vernal, 2007).

Currently, three calibrated modern dinocyst databases can be used (Fig. 4). Each of these dinocyst databases encompasses sediment samples that were processed with the same laboratory protocol (i.e. standardized palynological treatment, de Vernal et al., 1999; and Rochon et al., 1999; http://www.epoc.u-bordeaux.fr/index.php?lang=fr&page=eq_paleo_pollens) and with homogenized taxonomy (Fensome and Williams, 2004; Fensome et al., 2008, 2009). The current largest database, from the Northern Hemisphere, includes 1,492 sites (de Vernal et al., 2013a); the second one, mostly located between 30°N and 50°S, includes 237 sites (Marret et al., 2008; Hardy et al., 2018); and the third one, from the Southern Ocean, comprises 343 sites (Marret et al., 2001; Esper and Zonneveld, 2002; Crouch et al., 2010; Verleye and Louwye, 2010; Prebble et al., 2013). A small database is currently developed in the Black Sea region (Mudie et al., 2017) but has not yet been tested for past sea-surface reconstructions. In order to investigate and then validate the sensitivity of dinocyst assemblages to various marine surface environmental

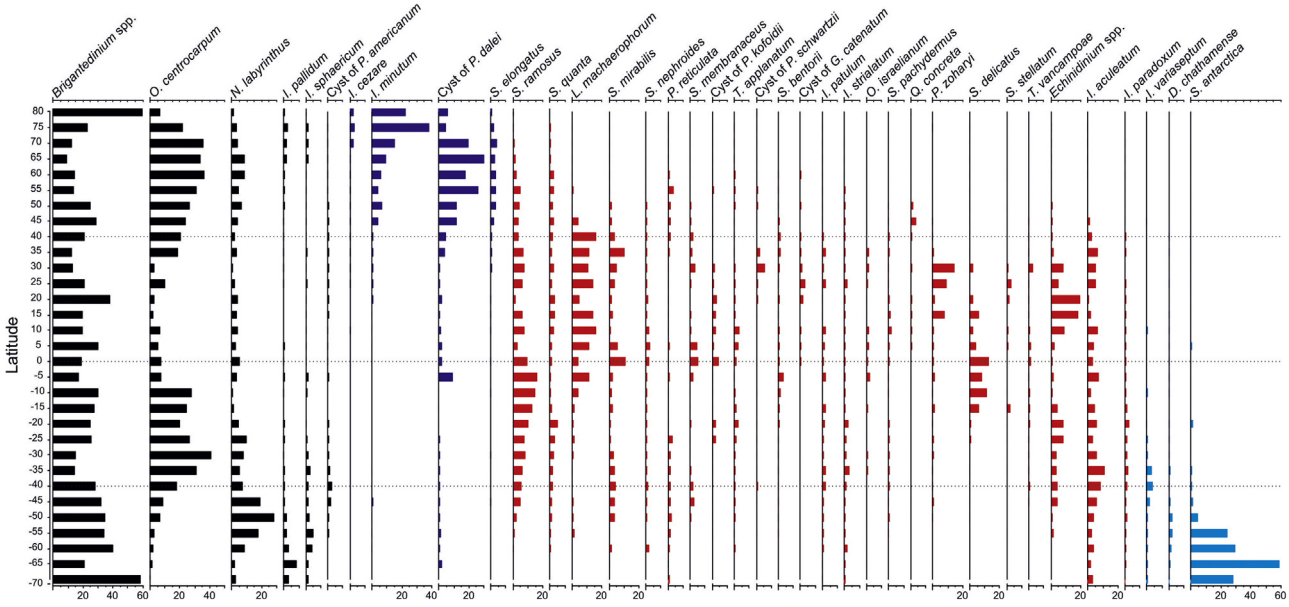

Fig. 3. Latitudinal distribution of the most abundant dinoflagellate cyst taxa from assemblages and diversity. Relative abundance for each species and diversity were averaged in a 5-degree latitudinal band.

Table 1
List of modern marine environmental parameters implemented in modern databases and used for dinocyst-based quantified reconstructions.

Environmental parameters	Source	Arctic database	Tropical Atlantic database	Austral database
Sea-Surface Temperature	World Ocean Atlas	v2001	v2013 IPSL-CM5A-LR model Preindustrial simulation	v2009
Sea-Surface Salinity	World Ocean Atlas	v2001	v2013	v2009
Sea-Ice Cover	National Snow and Ice Data Center 1953-2003 mean	X	–	–
Primary Productivity	Vertical Generalized Production Model (Behrenfeld and Falkowski, 1997) Remote-sensing spatial observations	2002-2005 mean, Aqua-Modis satellite	1978-2016 mean CZCS-SeaWifs-Modis space programs IPSL-CM5A-LR model Preindustrial simulation	–

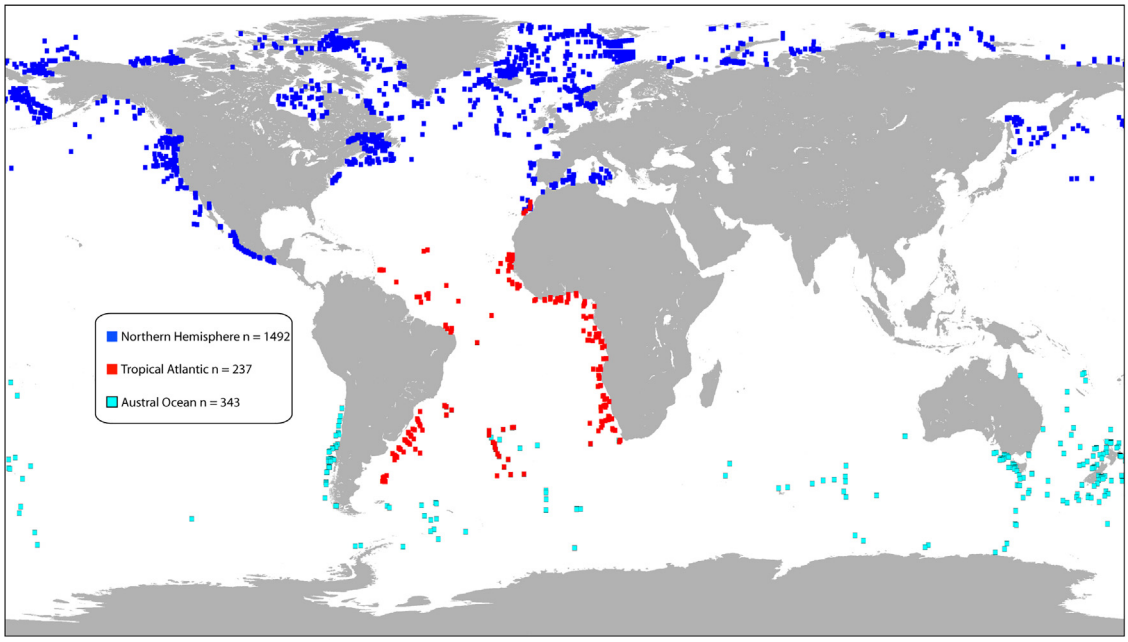

Fig. 4. Location of modern sites included in dinocyst modern databases used for quantified paleoceanographic reconstructions.

settings, multivariate analyses are routinely conducted, in particular Canonical Correspondence Analysis (CCA; de Vernal et al., 2001; Marret et al., 2008; de Vernal et al., 2013a). This method highlights the taxonomic statistical distribution shaped by the affinity of some groups of species with predefined environmental parameters (Fig. 5). For example, SIC (expressed in months.year^{-1}) strongly determines the distribution and abundances of *Islandinium? cezare*, *Islandinium minutum*, *Impagidinium pallidum* and *Islandinium brevispinosum* in the Arctic Ocean.

Although chosen environmental parameters (SIC, SSS, SST and NPP) control most of the modern assemblage variability, the CCA analysis does not evidence sometimes an obvious link between species and abiotic factors. This probably suggests that other variables are not yet taken into account, such as turbulence, light availability, for quantitative reconstructions, and may imply to add such information in the environmental dataset. This has been recently proposed for instance to discuss and quantify colder water involved in upwelling cell mechanisms along the western African margin by defining an upwelling index using local SST anomalies (SST at the local level compared with SST average at the regional latitudinal level) (Hardy et al., 2018). Also, other data derived from abiotic parameters could be added in the environmental dataset such as seasonality in SST, SSS or NPP. Finally, a wider range of abiotic parameters are also available within the World Ocean Atlas, including water density, dissolved oxygen, oxygen saturation and abiotic nutrient concentration, and could be tested through CCA analyses.

5. Paleoceanographic reconstructions for the last glacial cycle in the North Atlantic

5.1. The last glacial period

The last glacial was punctuated by rapid climate oscillations between cold (stadial) and warm (interstadial) atmospheric phases, known as the Dansgaard-Oeschger events (Dansgaard et al., 1993). The transition from stadial to interstadial phases is characterized by an abrupt warming of several degrees (up to 16 °C) in a few centuries (Kindler et al., 2014). These oscillations are thought to be linked to changes in the North Atlantic Ocean circulation and cryosphere dynamics. Interstadials are marked by a circulation pattern close to that of the present-day, i.e. a relatively active ocean circulation bringing warmth from low to high latitudes through a strong northward flow of warm surface waters by the Gulf Stream and its northward extensions (e.g., Rahmstorf, 2002). Stadials are associated with iceberg delivery resulting from the collapse of the northern hemisphere ice-sheets (e.g., Bond and Lotti, 1995). These surges appear similar, but occurred with a larger and wider extent, than the increasingly recurrent iceberg calving episodes occurring nowadays around Antarctica (e.g., Tollefson, 2017). They

Table 2
List of dinocyst taxa and their acronyms used in Fig. 5.

Code	Taxa name	Notes
ACHO	*Achomosphaera* sp.	
ALEX	Cf. *Alexandrium tamarense* cyst	
ATAX	*Ataxodinium choane*	
BSPO	*Bitectatodinium spongium*	
BSPP	*Brigantedinium* spp.	Sum of *Brigantedinium simplex*, *B. cariacoense* and undefined *Brigantedinium*
BTEP	*Bitectatodinium tepikiense*	
CYSA	Cyst Type A	
DCHA	*Dalella chathamense*	
DUBRI	*Dubridinium caperatum*	
EACU	*Echinidinium aculeatum*	Grouped into "ECHI" in n = 237 database
EDEL	*Echinidinium delicatum*	Grouped into "ECHI" in n = 237 database
EGRA	*Echinidinium granulatum*	Grouped into "ECHI" in n = 237 database
EKAR	*Echinidinium karaense*	
ETRA	*Echinidinium transparentum*	Grouped into "ECHI" in n = 237 database
ESPP	*Echinidinium* spp.	Grouped into "ECHI" in n = 237 database
ECHI	Sum of *Echinidinium* species	Specific to n = 237 database
GYMN	*Gymnodinium* sp.	
IACU	*Impagidinium aculeatum*	
IBRE	*Islandinium brevispinosum*	
IJAP	*Impagidinium japonicum*	
IMIC	*Islandinium cezare*	
IMIN	*Islandinium minutum*	
IPAL	*Impagidinium pallidum*	
IPAR	*Impagidinium paradoxum*	
IPAT	*Impagidinium patulum*	
IPLI	*Impagidinium plicatum*	
ISPH	*Impagidinium sphaericum*	
ISTR	*Impagidinium strialatum*	
IVAR	*Impagidinium variaseptum*	
IVEL	*Impagidinium velorum*	
LMAC	*Lingulodinium machaerophorum*	
LOLI	*Lejeunecysta oliva*	Grouped into *Lejeunecysta* spp. in n = 1492
LSAB	*Lejeunecysta sabrina*	Grouped into *Lejeunecysta* spp. in n = 1492
NLAB	*Nematosphaeropsis labyrinthus*	Includes *N. lemniscata* in n = 237 database
OAGU	*Operculodinium aguinawense*	
OCEN	*Operculodinium centrocarpum*	
OCSS	*O. centrocarpum* short processes	Split from "OCEN" only in n = 1492 database
OISR	*Operculodinium israelianum*	
OJAN	*Operculodinium janduchenei*	
OLON	*Operculodinium longispinigerum*	
PAME	*Protoperidinium americanum*	
PARC	*Polykrikos* sp. Arctic morphotype	
PDAL	Cyst of *Pentapharsodinium dalei*	
PERI	Protoperidinioids	
PKOF	*Polykrikos kofoidii*	
PNUD	*Protoperidinium nudum*	Grouped with *Selenopemphix quanta* in n = 237
PRET	*Pyxidinopsis reticulata*	
PSCH	*Polykrikos schwartzii*	
PZOH	*Polysphaeridium zoharyi*	
QCON	*Quinquecuspis concreta*	
SANT	*Selenopemphix antarctica*	
SBEL	*Spiniferites belerius*	Grouped with *Spiniferites membranaceus* (n = 237)
SBEN	*Spiniferites bentorii*	
SBUL	*Spiniferites bulloides*	Grouped with *Spiniferites ramosus* (n = 237)
SDEL	*Spiniferites delicatus*	
SELO	*Selenopemphix elongatus*	
SHYP	*Spiniferites hyperacanthus*	Grouped with *Spiniferites mirabilis* (n = 237)
SLAZ	*Spiniferites lazus*	
SMEM	*Spiniferites membranaceus*	
SMIR	*Spiniferites mirabilis*	
SNEP	*Selenopemphix nephroides*	
SPAC	*Spiniferites pachydermus*	
SQUA	*Selenopemphix quanta*	
SRAM	*Spiniferites ramosus*	
STEL	*Stelladinium* spp.	Sum of *Stelladinium stellatum*, *S. bifurcatus*, *S. robustum* and *S. reidii*
TAPP	*Trinovantedinium applanatum*	
TPEL	*Tectatodinium pellitum*	
TVAN	*Tuberculodinium vancampoae*	
TVAR	*Trinovantedinium variabile*	
VCAL	*Votadinium calvum*	
VSPI	*Votadinium spinosum*	
XXAN	*Xandarodinium xanthum*	

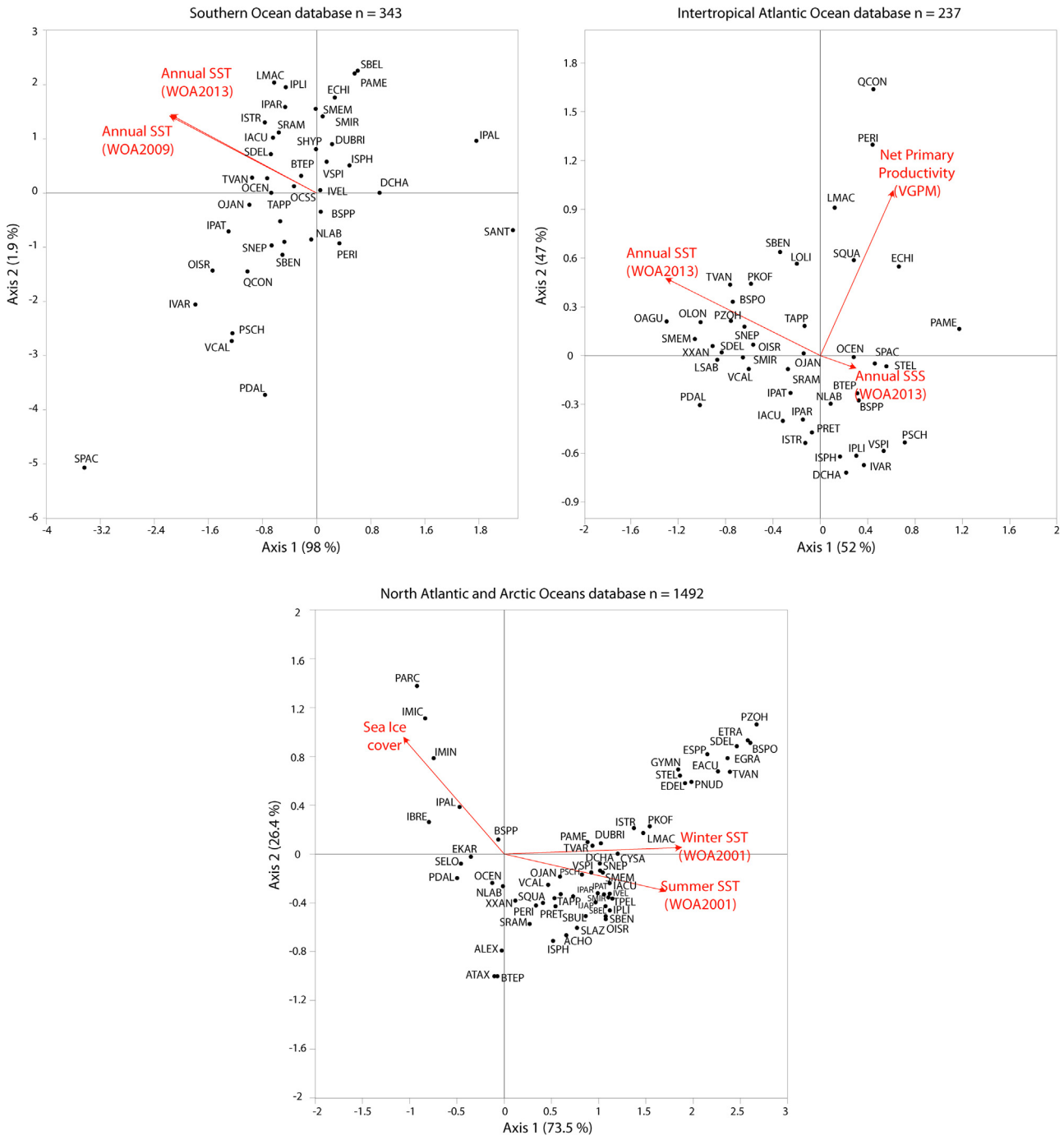
Southern Ocean database n = 343
Annual SST (WOA2013)
Annual SST (WOA2009)
Axis 1 (98 %)
Axis 2 (1.9 %)
Intertropical Atlantic Ocean database n = 237
Net Primary Productivity (VGPM)
Annual SST (WOA2013)
Annual SSS (WOA2013)
Axis 1 (52 %)
Axis 2 (47 %)
North Atlantic and Arctic Oceans database n = 1492
Sea Ice cover
Winter SST (WOA2001)
Summer SST (WOA2001)
Axis 1 (73.5 %)
Axis 2 (26.4 %)

Fig. 5. Canonical Correspondence Analyses (CCA) performed with PAST software (Hammer et al., 2001) on Arctic (de Vernal et al., 2013a, b), Tropical Atlantic (Marret et al., 2008; Hardy et al., 2018) and Southern Oceans (Prebble et al., 2013) modern databases. Taxa acronyms are listed in Table 2. SST: Sea-Surface Temperature; SSS: Sea-Surface Salinity; WOA: World Ocean Atlas.

are thought to be responsible for the coeval slowdown of the North Atlantic Ocean circulation (e.g., Rahmstorf, 2002). The most extreme iceberg calving episodes, whose influence reached latitudes as low as ca. 36°N (e.g., Cacho et al., 2001; Eynaud et al., 2009), are referred to as Heinrich events (Heinrich, 1988). These recurring climate changes, likely initiated in the high latitudes of the North Atlantic, thus also directly affected the mid and low latitudes of this basin. Through coupled ocean-atmosphere-cryosphere teleconnections, they also had worldwide repercussions imprinted as millennial oscillations of various components of the climate system and expressed at widespread locations, such as atmospheric temperatures in Antarctica, East Asian monsoon intensity, or North Pacific upwelling activity (e.g., Voelker, 2002). A huge effort has been undertaken through numerous sedimentological, micropaleontological, palynological, and geochemical studies of last glacial sedimentary archives to explore the underlying ocean-cryosphere-atmosphere-biosphere relationships and tentatively disentangle causal and consequential mechanisms.

5.2. *Sea-surface temperature and salinity information*

Dinocyst-based studies conducted in the North Atlantic Ocean and adjacent seas have contributed to shed significant light on oceanic-climatic coupled processes (e.g., cores and data in

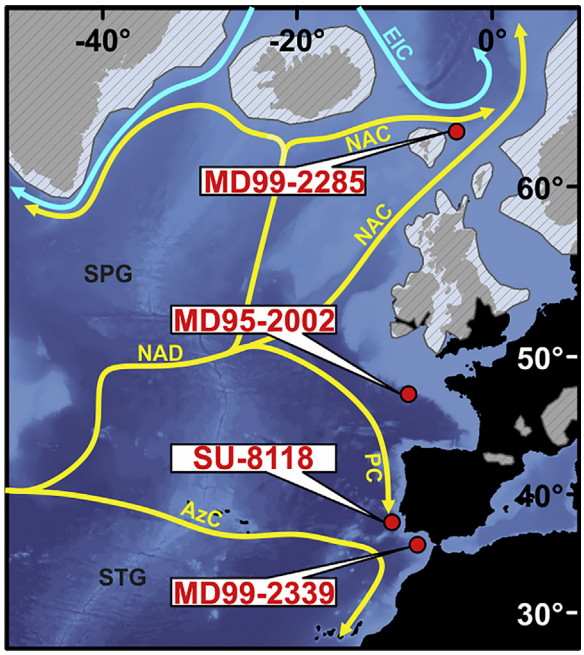

Fig. 6. Hydrographical context of the North Atlantic Ocean and location of the latitudinal transect of cores used in Fig. 7. The hatched areas represent the last glacial maximal extent of proximal ice sheets (after Ehlers and Gibbard, 2007). The arrows indicate the major pathways of warm surface waters (yellow) carried by the Gulf Stream northward extensions and cold polar waters (blue). AzC = Azores Current, PC = Portugal Current, NAD = North Atlantic Drift, NAC = North Atlantic Current, EIC = East Icelandic Current, STG = Subtropical Gyre, SPG = Subpolar Gyre.

Figs. 6 and 7). In the northeastern Atlantic Ocean (e.g., Zaragosi et al., 2001; Eynaud et al., 2012), along the path of the Gulf Stream extensions, millennial to infra-millennial stadial/interstadial shifts in ocean circulation were evidenced. Interstadials appear there to be characterized by the substantial influence of the warm northward inflow of surface waters from the Gulf Stream extensions. Indeed, core MD95-2002 (Bay of Biscay) allows to evidence higher SST (Eynaud et al., 2012) and higher abundances of *Operculodinium centrocarpum* sensu Wall and Dale, 1966 (Fig. 7b), whose modern distribution is tightly linked to the Gulf Stream northward extension pathways (e.g., Harland, 1983; Rochon et al., 1999), and conversely during stadials characterized by the southward migration of cold polar surface waters and increasing percentages of *B. tepikiense* (Fig. 7b). The influence of the iceberg delivery was also detected on the eastern side of the North Atlantic through SSS reconstructions that proved useful in tracking freshwater inputs resulting from both the melting of icebergs and European ice-sheets as well as the subsequent run-off that occurred on the Celtic margin (i.e. as evidenced through low SSS during stadials at site MD95-2002; Eynaud et al., 2012; Fig. 7b'). In the subpolar northwestern Atlantic and Labrador Sea, SST and SSS reconstructions also enabled to evidence severe cooling and freshening of surface waters that occurred during Heinrich events in response to iceberg surges (de Vernal and Hillaire-Marcel, 2000; Hillaire-Marcel and de Vernal, 2008).

Combined to seasonal SST contrasts, SSS reconstructions in the subpolar northeastern Atlantic Ocean and southern Norwegian Sea furthermore provided a valuable way to infer variations in the stratification of the upper water column. There, during stadials, stronger seasonal SST contrasts associated to the lower salinity surface layer suggest an increase in the stratification of the upper water column. This is materialized by a lower thermal inertia of the fresher surface layer in response to the coeval slowdown of the North Atlantic Ocean circulation (i.e. decreasing influence of the warm and salty surface waters of the Gulf Stream extensions) and concomitant meltwater inputs associated with the iceberg delivery (Zumaque et al., 2012; Wary et al., 2015, 2016, 2017). In the southern Norwegian Sea (core MD99-2285), this interpretation was qualitatively supported by the concomitant higher abundances of *B. tepikiense* (Fig. 7a), a taxon which presents a strong affinity for stratified surface waters associated with high seasonal contrasts (Rochon et al., 1999). Significant percentages of *B. tepikiense* also enabled to track the influence of Heinrich events as south as the southern Portugal (Turon et al., 2003; Penaud et al., 2011; core SU-8118, Fig. 7c). Also, even if not significant in Gulf of Cádiz assemblages (core MD99-2339), *B. tepikiense* percentages summed with those of *Spiniferites elongatus*, *Nematosphaeropsis labyrinthus*, cysts of *Pentapharsodinium dalei* and *Spiniferites lazus*, allowed to detect the Heinrich event impact in subtropical northeastern Atlantic waters by the establishment of a qualitative paleothermometer (cf. lower Warm/Cold ratio obvious during Heinrich events in Fig. 7d; Penaud et al., 2016).

5.3. Primary productivity changes

In the intertropical area, primary productivity changes are related to wind stress changes and the complex interplay between ocean current reorganization and upwelling cell dynamics, as well as to river discharges and associated nutrient inputs. Productivity regimes are crucial to reconstruct through time since they represent an additional mechanism to the physico-chemical carbon dioxide ocean-atmosphere exchanges, necessary to understand the carbon cycle that also involves the biological pump. Dinocyst-based quantitative studies have provided valuable information regarding productivity in the Congo Basin (Hardy et al., 2018, reconstructions made with the revised n = 208 tropical Atlantic database published in Marret et al., 2008, Fig. 4) as well as in the NE subtropical Ocean (Penaud et al., 2016, Fig. 7d': reconstructions made with the n = 1492 Northern Hemisphere database published in de Vernal et al., 2013a, Fig. 4). Today, proxies used for assessing primary productivity changes in the intertropical area are mainly represented by Total Organic Carbon, planktonic $\delta^{13}C$, and/or Biogenic Silica. However, calcareous and/or siliceous microfossils are extremely sensitive to dissolution through pH and temperature changes in the water column (e.g., Takahashi and Honjo, 1981; Barker et al., 2005; Barker, 2016; Charrieau et al., 2018), while organic-walled dinocysts are immune to the effect of dissolution, being more subject to oxidation issues (Zonneveld et al., 1997; Gray et al., 2017). Dinocyst-derived reconstructions of past primary productivity changes therefore provide one of the most significant observations in the intertropical area.

Considering the last glacial cycle and its recurring millennial climate changes, dinocyst analyses carried out in subtropical to tropical North Atlantic latitudes shed light on significant paleohydrological changes from the western (Vink et al., 2001; González et al., 2008) to the eastern Atlantic margins (southern Portugal: Turon et al., 2003; Eynaud et al., 2000; Penaud et al., 2011; western African margin: Marret and Turon, 1994; Marret et al., 2008; Holzwarth et al., 2010; Kim et al., 2010; Penaud et al., 2010, 2011, 2016; Hardy et al., 2016, 2018). Studies pointed to higher primary productivity conditions during glacial periods, and especially during stadials, as a result of increasing upwelling activity. This can be evidenced through increasing abundances of heterotroph dinocysts (mainly *Brigantedinium* spp.) as depicted by the Heterotroph/Autotroph ration in Fig. 7c' (core SU-8118), and conversely during interstadials (i.e. enhanced stratification related to stronger continental freshwater discharges and/or upwelling relaxation). In the Gulf of Cádiz, increasing annual productivity during the glacial period (core MD99-2339, Fig. 7d'), has been related to

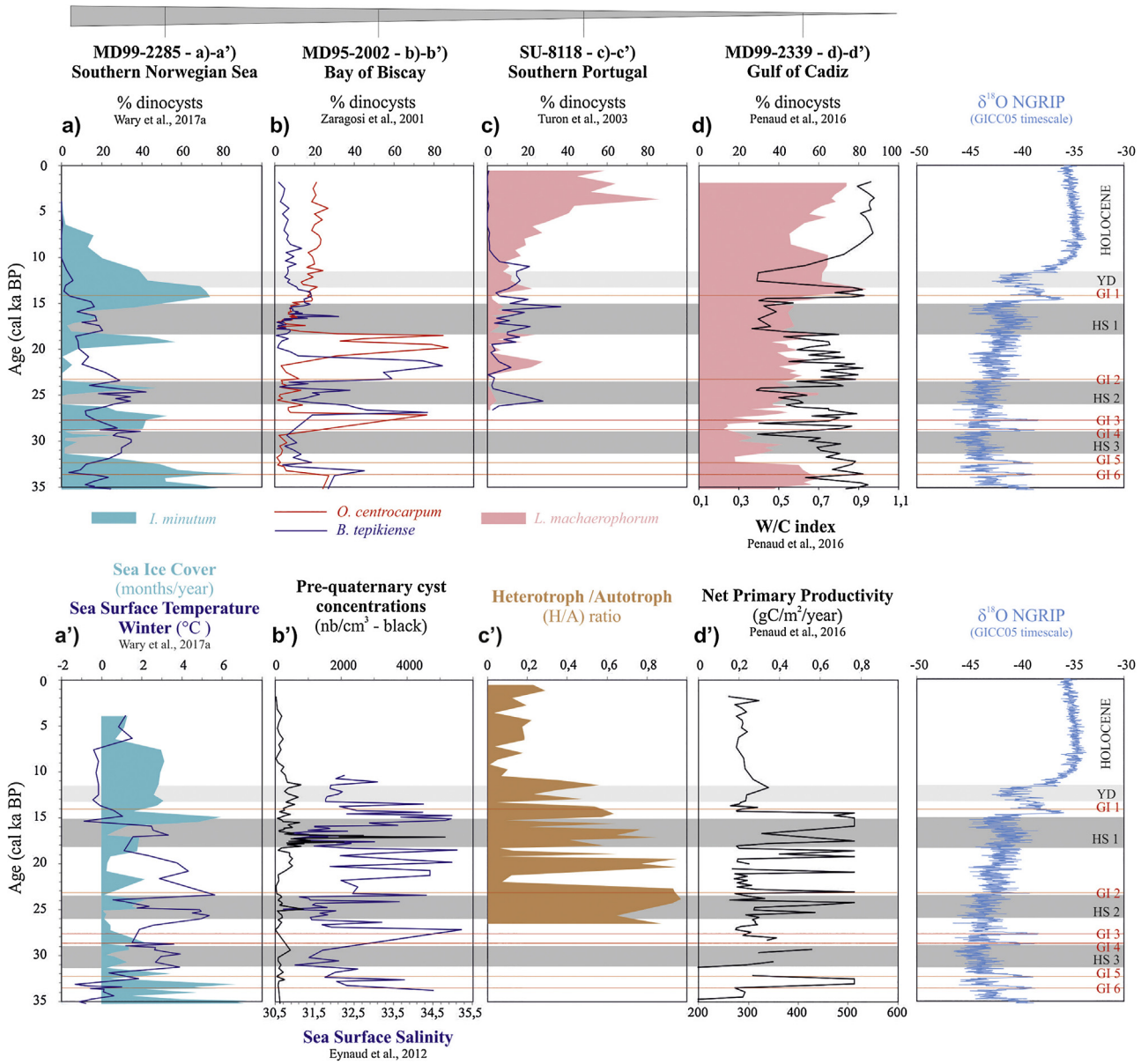

Fig. 7. Dinocyst data acquired in 4 different cores: MD99-2285 (a–a'), MD95-2002 (b–b'), SU-8118 (c–c'), MD99-2339 (d–d'), located in a north-south transect (cf. Fig. 6) in the NE Atlantic Ocean in parallel with Greenland $\delta^{18}O$ data (NGRIP, GICC05 timescale). Warm/Cold (W/C) index (cf. Penaud et al., 2016 for the species used to establish the ratio).

frontal system reorganizations within the Gulf of Cádiz resulting in local upwelling cells, especially during Heinrich events.

5.4. Past sea ice cover in the northern Hemisphere

Although sea ice is a parameter difficult to assess with paleoproxies (cf. de Vernal et al., 2013b), dinocysts offer the unique opportunity to get both qualitative indicators of sea ice (related to particular individual species, such as *Islandinium minutum*, whose highest abundances are found in cold polar waters seasonally covered with sea ice; Radi et al., 2013) and quantitative estimations of SIC duration and concentration (e.g., de Vernal et al., 2013a,b). Dinocyst data thus represent a valuable way to picture changes in sea-ice cover associated with the glacial millennial timescale variability, allowing to evidence significant SIC durations associated with the severe cooling recorded during Heinrich events in the subpolar northwestern Atlantic and Labrador Sea (de Vernal and Hillaire-Marcel, 2000; Hillaire-Marcel and de Vernal, 2008), as well as in the subpolar northeastern Atlantic (Caulle et al., 2013) and in the Bay of Biscay (Zaragosi et al., 2001; Auffret et al., 2002; Eynaud et al., 2012). In the Norwegian Sea, they have in contrast depicted a paradoxical pattern of sea-surface conditions, usually uncaptured or challenged by interpretations derived from the most commonly used planktonic foraminiferal data (e.g. Dokken and Jansen, 1999; Rasmussen and Thomsen, 2004; Dokken et al., 2013), where cold stadials are marked by warmer sea-surface conditions and reduced SIC (Eynaud et al., 2002; Wary et al., 2017a,b; cf. core MD99-2285 for the southern Norwegian Sea, Fig. 7a'). They have equally denoted a similar atypical pattern over the whole Nordic Seas during the LGM (de Vernal et al., 2005), pointing out here again discrepancies between different proxies of sea-surface conditions (de Vernal et al., 2006) that were also reported in other multiproxy studies (e.g., Penaud et al., 2011; Eynaud et al., 2012). In most cases, these discrepancies have been suggested to likely result from differences in ecological strategies between producers (e.g., de Vernal et al., 2006; Wary et al., 2015, 2017a). Dinoflagellates, as well as

coccolithophorids or diatoms, are mostly restricted to the uppermost 50 meters of the water column (e.g. Sarjeant, 1974). In contrast, the symbiont-free planktonic foraminiferal taxa composing assemblages of these area and period have the ability to adapt their depth habitat and migrate deeper (e.g., Schiebel et al., 2001), especially if surface conditions are not favorable to their development such as the low SSS that prevailed in this basin during these periods. Taphonomic biases related to preferential allochtonous advection of smaller and lighter planktonic remains (such as dinocysts) could also be implied (e.g., de Vernal et al., 2006). Even if unlikely in the case of the glacial Nordic Seas (Eynaud et al., 2002; Wary et al., 2016), such biases (as well as others related to seasonality of the growth season and/or interannual variability; e.g., de Vernal et al., 2005; Penaud et al., 2010) must always be kept in mind when using dinocysts in paleoceanographic studies.

5.5. Pre-Quaternary dinocysts as erosion tracers

From another point of view, advection of allochtonous dinocysts may provide valuable insights in the framework of paleoreconstructions. In the case of the last glacial rapid variability, pre-Quaternary dinocysts, absent in most surface sediments from the North Atlantic but encountered in continental rocks overlaid by ice-sheets during the last glacial period, were used to track the geographical origin of icebergs during Heinrich events (Rahman, 1995). Maximal fluxes of these reworked palynomorphs, sometimes illustrated through high values of the "pre-Quaternary *versus* modern dinocysts" ratio or of pre-Quaternary cyst concentrations, were correlated to Heinrich event iceberg surges in the Labrador Sea (Gibb et al., 2014), while on the Celtic Margin and in the southern Norwegian Sea, they were attributed to intense melting and subsequent freshwater inputs from proximal ice-sheets (Zaragosi et al., 2001; Eynaud et al., 2007; Penaud et al., 2009; Wary et al., 2018). The highest values of pre-Quaternary cyst concentrations at the beginning of Heinrich event 1 are coeval with very low SSS values, thus depicting strong glacio-fluvial inputs from the European ice-sheets at that time (core MD95-2002, Fig. 7b'). On the Celtic margin, which is located at the outlet of the Manche paleoriver, such interpretation was supported by concomitant high relative abundances of *L. machaerophorum*, often found near river mouths (e.g., Zonneveld et al., 2013; maximal percentages recorded today in southern Portugal and in the Gulf of Cádiz, Fig. 7c and 7d), and high concentrations of coenobia of the freshwater microalgae *Pediastrum* spp. (Zaragosi et al., 2001; Auffret et al., 2002; Eynaud et al., 2007; Penaud et al., 2009).

6. Dinocyst-based paleoecological reconstructions on coastal eutrophicated areas

Moving from the oceanic domain to littoral environments, coastal and estuarine areas are constantly evolving, shaped by natural dynamic agents and anthropogenic impacts. Since the 1980s, international efforts have been undertaken to evaluate the magnitude and severity of present changes occurring along world's coastal areas. Resulting assessments pointed to a generalized disturbance of all coastal areas, whatever the oceans or seas they border (e.g., Tilman et al., 1994; Rabalais et al., 2009; IPCC, 2014). These changes are particularly relevant to shoreline development, surface water quality (i.e. temperature, salinity, nutrient concentration, industrial pollution) and marine organisms (i.e. biodiversity changes, invasive species). Due to increasing urbanization and agriculture growth, nutrient pollution has become a major concern in many coastal regions (e.g., Carpenter et al., 1998; Rabalais, 2002; Price et al., 2017b). For example, over 65% of US estuaries are considered as moderately to highly eutrophicated (Bricker et al., 2008). The effect of soil fertilization on the composition and structure of microbial coastal communities is indeed one of the major topics of present-day environmental sciences, taking into account that changes in temperature, moisture or nutrient rates are assumed to greatly affect biodiversity over many trophic levels (Diaz and Rosenberg, 2008). The currently accepted definition of eutrophication by Nixon (1995) is: « *the process of increased organic enrichment of an ecosystem, generally through increased nutrient inputs* ». Initially used to designate the natural nutrient enrichment, the term has recently been used to refer to human influences accelerating eutrophication of rivers, estuaries, or marine waters. Sources of anthropogenic activities include the leaching of agricultural fertilizers, land run off, sewage inputs, combustion of fossil fuels and nutrient excess from aquaculture (Glibert et al., 2005; Smayda, 2008). Human activities indeed contribute to the acceleration of nutrient enrichment over the last century with increased nitrogen and phosphorus inputs, thereby altering phytoplankton production and community structuring (e.g., Turner and Rabalais, 1994; Glasgow and Burkholder, 2000; Anderson et al., 2008).

Dinocysts are known to reflect anthropogenic changes and few studies have tried to link dinocyst distribution pattern to different pollution types. Most studies focused on the effect of nutrient enrichment on the dinoflagellate community and the potential of organic-walled dinoflagellates as eutrophication indicators in coastal waters (e.g., Dale and Fjellså, 1994; Dale et al., 1999; Dale, 2001, 2009; Pospelova et al., 2002, 2004; Matsuoka et al., 2003; Sangiorgi and Donders, 2004; Pospelova and Kim, 2010; Kim et al., 2012; Tian et al., 2018), although few areas were studied testing the effects of industrial pollution (e.g., Sætre et al., 1997; Dale, 2001; Pospelova et al., 2005; Liu et al., 2012; Aydin et al., 2015; Triki et al., 2017). Numerous studies showed that eutrophication signal can be identified by increased dinocyst concentrations in sediments along with nutrient input increases (Dale and Fjellså, 1994; Dale et al., 1999; Matsuoka, 1999; Persson et al., 2000; Pospelova et al., 2005; Rabalais et al., 2009; Liu et al., 2012; Zonneveld et al., 2012). However, Pospelova et al. (2002), in New Bedford Harbor and Apponagansett Bay (Massachusetts, USA), revealed that the observed increase in dinocyst taxa diversity from oligotrophic to mesotrophic conditions is followed by a decline in taxa richness when hypertrophic conditions occurred (i.e. extremely high nutrient levels); a "highly eutrophicated threshold" would then lead to an opposite effect on diversity. In addition, heterotrophic dinoflagellates positively react to increasing coastal water eutrophication, especially Protoperidinioids, Polykrikaceae, and diplopsalioideans (e.g., Thorsen and Dale, 1997; Matsuoka, 1999; Matsuoka et al., 2003; Kim et al., 2009; Krepakevich and Pospelova, 2010; Pospelova and Kim, 2010). It has been suggested that significant nutrient supplies from continental river runoff entailed the heterotrophic dinoflagellate population abundance by promoting diatom biomass production, thus enriching the prey stock (Matsuoka, 1999; Godhe and McQuoid, 2003; Kim et al., 2009). Dale (2001) also linked heterotrophic dinoflagellate increases to the reduced production of autotrophic dinoflagellates, in a context of decreasing light penetration.

Concerning specific taxa, *Lingulodinium machaerophorum* has often been shown to be sensitive to cultural eutrophication in estuarine environments and shows relative and absolute abundance increases along with the growing eutrophication in most studied environments (e.g., Dale and Fjellså, 1994; Dale et al., 1999; Sangiorgi and Donders, 2004; Dale, 2009; Harland et al., 2010; Shin et al., 2010; Zonneveld et al., 2012). However, regarding the whole dinoflagellate community, there is no consensus on a fossil dinocyst assemblage-type that would reflect nutrient enrichment in disturbed estuarine environments (Pospelova et al., 2002). Price et al. (2017b) concluded that there is no single species that characterizes eutrophic estuaries or high nutrient loading. Large fluctuations in

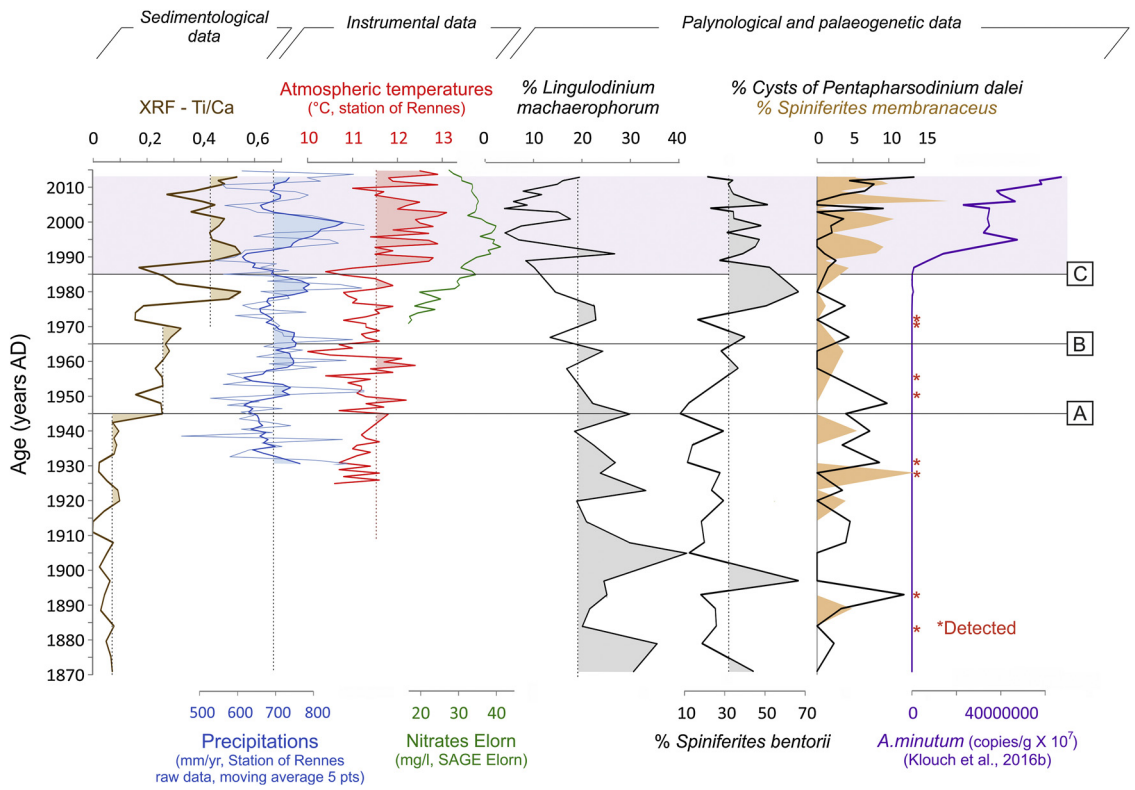

Fig. 8. Comparison between selected palynological data from the I_09 core taken in a highly anthropized estuary (Bay of Brest, Brittany; Lambert et al., 2018), data from ancient DNA measurements (Klouch et al., 2016), and instrumental data from in situ measurements in watersheds. From left to right: XRF Ti/Ca ratio from the study core, measured precipitations and atmospheric temperatures (Rennes meteorological station; infoclimat.fr), measured nitrate fluxes in the Elorn river (SAGE Elorn), dinocyst percentages (*Lingulodinium machaerophorum*, *Spiniferites bentorii*, cysts of *Pentapharsodinium dalei* and *Spiniferites membranaceus*) and detection curve of *Alexandrium minutum* species in the same core (from Klouch et al., 2016). Limit A corresponds to the first detection of continental runoff increases following the post-World War II land consolidation policy. Limit B corresponds to an increase in continental runoff and the massive introduction of nitrates for agricultural uses. Limit C highlights the top interval characterized by the preponderance of eutrophication indicators (i.e. nitrates fluxes) and significant changes in the dinoflagellate community: i) specific relay leading to the prominence of *S. bentorii*, *S. membranaceus* and cysts of *P. dalei*, and ii) the sharp increase of the *A. minutum* signal.

cyst production are then frequently observed and amplified by the abrupt increase of one or two regionally specific taxa (for example *Spiniferites* spp.: in New Bedford Harbour, NE USA, Pospelova et al., 2002, as well as in the Bay of Brest, NW France, Lambert et al., 2018). Pospelova et al. (2002) stated that taxa considered as eutrophication markers in the Norwegian fjords show very different responses in shallow coastal US estuaries, also highlighting that *L. machaerophorum* does not respond positively to human eutrophication acceleration in US estuaries contrary to deep Norwegian fjords where stronger impacts on water mass stratification are observed. Recent studies indeed show that an increase of cultural eutrophication can have negative influences on *L. machaerophorum* abundances (Lambert et al., 2018 in NW France, Fig. 8; García-Moreiras et al., 2018 in NW-Spain). Differences in geomorphology, hydrology, temperature and salinity between eutrophic estuaries thus result in different taxa responses to eutrophication (Price et al., 2017b). At the same time, some authors have shown that higher water temperatures could increase the vertical stability and influence the growth rates and the metabolism of the autotrophic dinoflagellates, contributing to increasing cyst production at the end of blooms (Godhe and McQuoid, 2003; Elshanawany et al., 2010) and highlighting the combined action of natural climatic variability and human-induced eutrophication on recent dinocyst concentration increases.

Furthermore, Dale (2001, 2009) pointed out that dinocysts show different responses to nutrient enrichment and industrial pollution. Indeed, several authors also noticed that if nutrient enrichment significantly increases the dinocyst abundances, industrial pollution decreases their abundances or changes the heterotrophic/autotrophic ratio (Sætre et al., 1997; Liu et al., 2012). Liu et al. (2012) showed that autotrophic cysts react more sensitively to industrial pollution than heterotrophic ones, even if the physiological mechanisms behind this difference remain unclear. Some authors then hypothesize that toxic compounds could affect the vegetative cell physiology, inducing a decrease of cell proliferation and an enhancement of cyst production rates so as to survive in unfavorable environmental conditions, with more difficulties to germinate under high metal concentrations in the water column (Lage et al., 1994; Okamoto and Colepicolo, 1998; Godhe and McQuoid, 2003; Leitão et al., 2003; Liu et al., 2012; Herzi et al., 2013, Aydin et al., 2015; Triki et al., 2017).

7. Perspective works: the potential of the ancient DNA for the reconstructions of dinoflagellate dynamics

In parallel with micropaleontological studies, innovative studies targeting the ancient DNA quantification are increasingly used in paleoecological and paleoenvironmental studies. The idea that the DNA retrieved in ancient sedimentary archives (ancient DNA) can be preserved for long periods of time has long been considered impossible because of the fragility of the DNA molecule and its rapid degradation by microorganisms. Indeed, when in its hydrated form, the DNA is subject to numerous abiotic (hydration, oxidation, UV damage) and biotic (microbial nuclease) degradation processes that lead to its fragmentation (Willerslev and Cooper, 2005). Despite its potential degradation, DNA has been shown to be well preserved in cold, dry environments such as permafrost and glaciers (Willerslev et al., 2004, Orlando et al., 2013) and under anoxic conditions

(Boere et al., 2011). Other physical factors such as low temperature, high pressure and high salinity also contribute to the preservation of DNA in sediments (Boere, 2010). DNA retrieved in marine sediment archives can be of different types and origins. After cell death or release into water, DNA molecules can undergo different transformations along the water column and in sediments, and eventually be degraded through biotic and abiotic processes and/or finally be preserved over the long term (Torti et al., 2015). Part of this DNA is deposited in marine and lacustrine sediments, either intracellularly (inside cells or dormant forms) or extracellularly (free outside cells). The resting forms of dormant organisms (cysts, spores, plant seeds, pollen) in sediments are thought to better preserve their DNA compared to organisms that do not have such resting stages. However, extracellular DNA has been shown to make up the bulk of total DNA in sediments and is generally associated with dead cells, organic and inorganic aggregates, and mineral matrices (Boere, 2010). In addition, it can protect against degradation by adsorbing to mineral matrices and refractory organic molecules (Pietramellara et al., 2009). It is estimated that between 50–95% of the extracellular DNA could be protected against degradation (Danovaro et al., 2006, Dell'Anno et al., 2002). In addition, a part of the DNA corresponds to living organisms in the sediments.

Under ideal conditions of preservation (permafrost and ice), the theoretical limit for conserving old DNA is estimated at around one million years (Allentoft et al., 2012). However, the longest duration observed in these environments was 400,000 to 800,000 years (Willerslev et al., 2007). Recently, studies have shown that ancient DNA can be very well stored under oxic conditions (Lejzerowicz et al., 2013, Coolen et al., 2013, Capo et al., 2016). This demonstrates the potential of DNA as a paleoecological tool even in a variety of ecosystems and biological research domains. Ancient DNA has been studied since Poinar et al. (1998) isolated for the first time 20,000-year-old (plant and animal) DNA traces from coprolites (fossilized excreta). Since then, there has been a drastic increase in studies that have integrated ancient DNA analysis into paleoecological studies. Indeed, ancient DNA has been used to answer a variety of questions, such as paleoenvironments (de Bruyn et al., 2011; Willerslev et al., 2014), species biogeography and evolution (Mitchell et al., 2014), population dynamics and extinction processes (Shapiro, 2004; Drummond et al., 2005), or human evolution, diseases and dietary shifts (Green et al., 2010; Meyer et al., 2012; Adler et al., 2013; Krüttli et al., 2014; Metcalf et al., 2014). Ancient DNA has been used to reconstruct past environments and assess ecosystem changes over time but also to reconstruct changes in biological communities such as viruses dating back to 7,000 years in the Black Sea (Coolen, 2011), bacteria dating back to 217,000 years in the Mediterranean (Coolen and Overmann, 2007), mushrooms of at least 16,000 years (Lydolph et al., 2005, Bellemain et al., 2013), plants of at least 10,000 years old (Parducci et al., 2013, Pedersen et al., 2013), and animals (mammoths and horses) of at least 7,000 years old (Haile et al., 2009). Regarding planktonic organisms, several studies showed that ancient DNA can be conserved across the Pleistocene timescale in various environments, from lakes to marine ecosystems. Indeed, the analysis of sediment cores taken at 5,000 m water depth in the Atlantic Ocean off Brazil (Lejzerowicz et al., 2013) and at 900 m in the Black Sea (Coolen et al., 2013) allowed recovering ancient DNA sequences of dinoflagellates, coccoliths, foraminifera and copepods up to 32,500 years old. Ancient DNA has been used to study dinoflagellate and haptophyte successions in the Arctic, Antarctic, Black Sea and Mediterranean sediments (Boere et al., 2011, Coolen et al., 2006; D'Andrea et al., 2006), allowing to reconstruct ancient planktonic community dynamics and their responses to environmental changes (e.g., Boere et al., 2011; Domaizon et al., 2013; Lejzerowicz et al., 2013; Coolen et al., 2013; Pawlowska et al., 2014; Capo et al., 2016; Li et al., 2016).

In the northwestern part of France, and more specifically in a highly anthropized estuary (Bay of Brest, Brittany), ancient DNA has been collected to reconstruct the invasive pattern of the potentially toxic dinoflagellate *Alexandrium minutum* over a time scale of almost 150 years (Klouch et al., 2016). The presence of *A. minutum* was indeed detected by quantitative PCR (qPCR) using specific primers (ITS rDNA) with an upsurge since the 1980s (Klouch et al., 2016; Fig. 8). *A. minutum* is one of the major toxin producers leading to the toxification of shellfish resources making their consumption dangerous. It is a widely distributed, coastal species that has been associated with paralytic toxins like saxitoxins (Taylor et al., 1995; Landsberg, 2002; Aylagas et al., 2014). Thanks to a multi-proxy approach combining paleogenetic and palynological (dinocysts and pollen grains) carried out at a very high (annual) resolution (Lambert et al., 2018), increasing abundances of *A. minutum* since the 1980s has been associated to a warming climate trend superimposed on changes in Bay of Brest agriculture practices in watersheds (Fig. 8). Changes in the structure of the dinocyst community observed in the Bay of Brest (i.e. major trophic relay between *L. machaerophorum* and *S. bentorii* around 1965 followed then by *S. membranaceus* around 1985 observed by palynological analyses), and the intensification of toxic algal blooms (i.e. *A. minutum*, detected by genetic analyses), both appear directly correlated to increasing atmospheric temperatures as well as increasing fertilizers (nitrates) for agriculture over the past decades in Bay of Brest watersheds (Fig. 8).

8. Conclusion

About 15% of dinoflagellates (aquatic protists) are known to produce resting cysts (dinoflagellate cysts or dinocysts) with morphology generally species-specific allowing to reconstruct paleoenvironments at different timescale over several (tens to hundreds of) millions of years (from the Middle Triassic, 240 Ma), (tens to hundreds of) thousands of years, to the pluridecadal timescales of human temporal perception.

Regarding the growing concerns about current climate change, dinocysts constitute a valuable tool to better understand ocean and climate variability, shed light on ecosystem responses to rapid climate changes and/or environmental perturbations, and to provide quantitative data needed to further constrain and validate models that are used for near-future climate simulations.

Furthermore, palynological studies conducted in parallel with paleogenetic studies could help to disentangle driving mechanisms responsible for recent changes in the structure of phytoplankton communities affecting coastal ecosystems, and especially causes responsible for the strong development of toxin-producing species under increasing influence of anthropogenic activities on watersheds.

Disclosure of interest

The authors declare that they have no competing interest.

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